The Zoogeographic Relationships of Fanning Island Inshore Fishes[1]

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REPRESENTATIVE FANNING ISLAND INSHORE FISHES were collected by means of rotenone poisoning in January 1970. The collections were made with the objective of elucidating the zoogeographic relationships of the Line Islands fish fauna. The results are presented here.

Zoogeographically, the Central Pacific forms an eastward extension of the great Indo-West Pacific faunal region centered today in the Austro-Malayan-Philippine area. The series of island archipelagos somewhat south of the equator and extending eastward without major breaks from New Guinea to the Tuamotus would seem to provide the axis of this extension. To the eastward along this axis or to the north or (presumably) south of it, the size of the fish fauna diminishes.

Paralleling this east-west axis along its subtropical borders to the north and south are, apparently, further small components of the Austro-Malayan fish fauna which, in the Central Pacific, do not seem to be represented in the tropics. McCosker (1970) mentions some of the forms comprising the southern subtropical band. *Microcanthus strigatus* in Hawaii would seem to represent such a northern, again subtropical, component. Also along the northern border occurs the extensive endemism of the fishes in the Hawaiian chain (Gosline and Brock, 1960). This Hawaiian endemism, associated at least in part with the isolation of the Hawaiian chain, does not seem to be counterbalanced by any similar area on the southern border of the Central Pacific tropics.

The above summary of Central Pacific fish zoogeography can be pieced together from scattered records, as has indeed been done by Fowler (1928), Ekman (1935), etc. Refinement of these general concepts must come from analyses of more quantitative data. For the Central Pacific, such data are few. Fishes of this region living at depths of more than 100 feet of water are practically unknown, and even the records of those that normally occur between 20 and 100 feet provide primarily a zoogeography of collectors. At Fanning no attempt was made to obtain fishes that could not be taken by rotenone from shore, and "inshore" fishes, as that term is used throughout this paper, will refer only to such forms.

But even among these fishes, there are relatively few areas in the Central Pacific that have been collected with sufficient thoroughness to make their data even approximately comparable. All such areas happen to lie in what may be considered the northeast quadrant of the Central Pacific north of the equator, bordered on the west by the Marshalls, on the north by the Hawaiian chain, and on the east by the Line Islands (Fig. 1). The present paper will, of necessity, deal almost entirely with this portion of the Central Pacific.

The analysis that follows is addressed to two questions: (1) the relative sizes of the inshore fish faunas of the islands in this quadrant, and (2) their interrelationships. With regard to diversity, it should be stated at the outset that, for one or more reasons, no two sets of the following figures are based on strictly comparable data. Nor are the data profitably refinable.

In the two major and several minor poison stations run at Fanning in January 1970, 143 species of inshore fishes belonging to 34 families were collected. If, to these, other University of Hawaii collections made at inshore stations on Palmyra and Christmas are added, then the counts for the Line Islands are raised to 235 species in 40 families.

In the Marshalls at Bikini, Schultz et al. (1953–1966) collected and reported on some 279 "inshore" species belonging to 52 families. So far as fishes are concerned, Bikini is probably the most intensely collected island in the Pacific. Prior to the atomic testing there a whole

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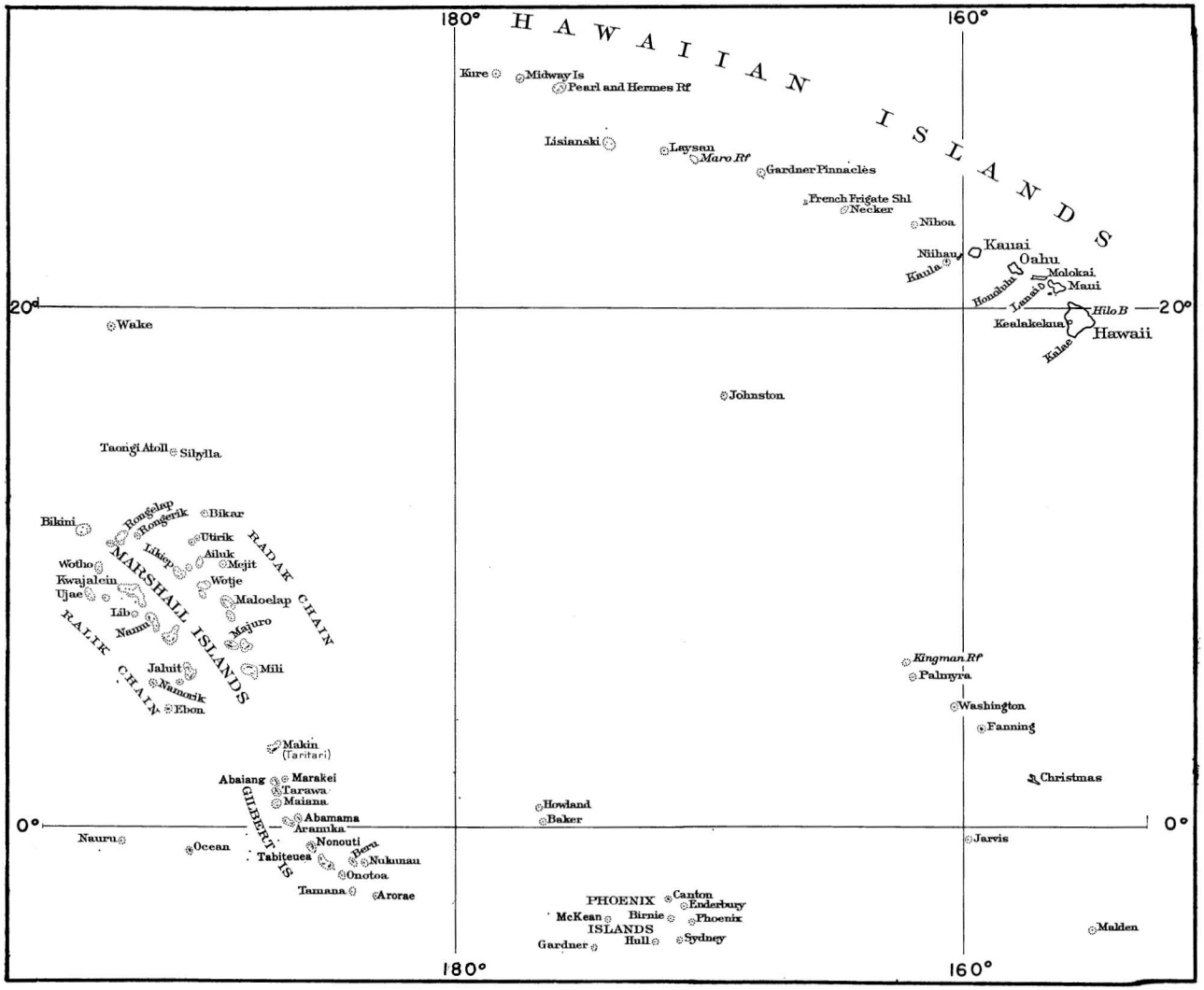

FIG. 1. Chart of island groups in the northeast quadrant of the Central Pacific. From U.S. Hydrographic Chart 1500, 47th edition, after Gosline, 1955.

troop of ichthyologists scoured the island for a full summer. A better basis of comparison with the Line Islands collections is perhaps Arno in the southern Marshalls, where Strasburg (1953) with relatively little assistance collected, during one summer, 250 species belonging to 51 families. A tentative conclusion would be that the Line Islands inshore fish fauna is somewhat, but not much, smaller than that of the Marshall Islands.

If the fishes of the Hawaiian chain are compared with those of the Line Islands, a difficulty again arises of finding a basis for comparison. In 1965 (in the first three columns of Table 1) the present author listed, from selected Hawaiian stations, 102 species belonging to 34 families. At Johnston, a well-collected outlier of the Hawaiian chain, 184 species (mostly inshore forms) belonging to 46 families have been recorded (Brock, Jones, and Helfrich, 1965). Still another basis for comparison is as follows. In all of the collections from inshore stations made around Oahu by the author of the present paper, the maximum number of species taken has been 75; at the two major Fanning Island stations, the numbers of species collected were 90 and 97. The conclusion seems justified that the diversity of inshore fishes in the Hawaiian chain is lower than that of the Line Islands.

As to relationships, the Line Islands fish fauna is basically of the Central Pacific type as represented at the Marshall Islands. A detailed comparison of available Line Islands fishes with those reported from the northern Marshalls by Schultz et al. (1953–1966) gives the following results.

Of the 235 Line Islands species, 25 are gobies and eleotrids. The material of these two groups from the northern Marshalls has not yet been worked up and must be excluded from further consideration. Of the remaining 210, all but 14 were recorded from the northern Marshalls by Schultz et al. (1953–1966). The remaining 14 can provisionally be divided into four categories. First there is the possibly endemic element. Aside from gobies and eleotrids, I have been unable to identify three of the Line Islands species collected: one *Parapercis,* one *Dascyllus,* and one *Scorpaena.* However, these may not be new species or, if they are, they may represent forms also present but as yet unrecorded elsewhere. Three other species may be mentioned in connection with possible endemism in the Line Islands area. *Istiblennius afilinuchalis,* described from the adjacent Phoenix Islands, seems to be as yet unrecorded elsewhere. It occurs in the Line Islands collections. However, the Line Islands specimens appear to differ little, if any, from the Marshallese *I. rodenbaughi. Pomacentrus aureus,* a very distinctive fish, was also described from the Phoenix group. It appears in the Line Islands collections and has been recorded by Randall (1953) from the Gilbert Islands southeast of the Marshalls. *Glossogobius tongarevae* was described from Tongareva somewhat to the south of the Line group. I have collected what appears to be this species in the Line Islands and Hawaii. To summarize, if any endemism occurs among the inshore fishes of the Line Islands area it is minimal.

Five species of Line Islands fishes would seem to represent a southern element that does not occur in the northern Marshalls: *Myrichthys elaps, Choeroichthys sculptus, Holocentrus violaceus, Lutjanus vaigiensis,* and *Zebrasoma rostratus.* All of these except the last are present in the Indo-Australian region. *Zebrasoma rostratus* seems to have been validly recorded only from the Tuamotus and perhaps the Society Islands to the southeast of the Line Islands (Randall, 1955).

Three species collected in the Line Islands have wide distributions in Hawaii and elsewhere but have not been recorded from the northern Marshalls: *Albula vulpes, Chanos chanos,* and *Muraena pardalis.*

Finally, one Hawaiian "endemic," *Apogon menesemus* (not the related Marshallese *A. menesemops*), was collected in the Line Islands.

The Line Islands inshore fish fauna may perhaps be summarized as a fairly representative assemblage of Central Pacific fishes of the northern Marshallese type, but with certain small additional elements that appear to have come in from the southwest, southeast, and north. Indeed, the only direction from which no Line Islands fishes came is the great space of open water to the northeast that extends from the Line Islands without a break to America.

That the Line Islands provide a sort of communications center for Central Pacific fishes is again suggested by data of a different sort. In 1948 Schultz and Woods showed that, in the *Acanthurus triostegus* complex, the pectoral markings of the Marquesan and Hawaiian forms differed from one another and from the typical Indo-Pacific form. Gosline (1955) pointed out that all three types of pectoral markings were at least partially represented in Line Islands specimens of *Acanthurus triostegus*. In the same species Randall (1956) demonstrated that the size at transformation from the larval stage of the Phoenix and Line islands form was intermediate between that of Hawaii and that of the northern Marshalls. Further data from the Line Islands bear this out.

The information that has just been presented will be used as a basis for developing the general thesis that the distributions of Central Pacific inshore fishes are primarily determined by the ecological factors around islands and not by the open-water areas between islands.

It seems best to start with the dispersal aspect of this thesis. The Central Pacific islands are of an oceanic nature, and there is no evidence that they were more closely spaced in the Cenezoic era than they are today (Menard, 1964). The presence of inshore fishes on these islands is therefore an a priori argument that they were somehow able to cross the open-water areas between islands. (That man has carried these inshore fishes between islands can, I think, be ruled out except in a few instances.) The question of whether open-water barriers have played a role in limiting the distributions within the Central Pacific of some fishes but not others can best be approached through an examination of the Hawaiian forma, for the Hawaiian chain is the most isolated archipelago in the Central Pacific, and, indeed, in the world. By Central Pacific standards, the inshore fish fauna of Hawaii (including Johnston) is fairly harmonic (Gosline and Brock, 1960). Central Pacific species with, and those without, planktonic larval stages are in Hawaii. Large Central Pacific species and minute ones are represented, however improbable it might seem that such a fish as *Eviota epiphanes,* with a maximum length of less than an inch, should have reached there.

Since an essentially harmonic representation of Central Pacific fishes is present on Hawaii it will be hypothesized that the various groups of Central Pacific fishes have approximately equal abilities to cross open-water areas, or at least that they all have the ability to cross any such barrier that occurs between island groups in the Central Pacific.

Support for the view that the open water surrounding the Hawaiian chain does not form an insuperable barrier for inshore fishes is provided by certain recent records. Thus, a number of years ago a large specimen of the very conspicuous *Pomacanthus imperator* was recorded from Hawaii (Brock, 1948), but no other member of the species has been seen. In 1951 Gosline and others made extensive collections at Johnston. No specimens of the distinctive *Megaprotodon strigangulus* were seen or taken. In 1964 the species was abundant at Johnston (Brock, Jones, and Helfrich, 1965), and a few specimens have since been taken on Oahu.

That species straggle out of, as well as into, the Hawaiian Islands is suggested by the Line Islands records of *Apogon menesemus* mentioned earlier.

The information presented suggests that at the present time a continuous interchange is taking place between Hawaiian fishes and those of the nearer Central Pacific islands.

There are perhaps three major reasons why the deep water between islands has been postulated as limiting Central Pacific inshore fish distribution. The first of these is the absence of a few widespread Central Pacific genera, e.g., *Lutjanus,* from Hawaiian waters. A second is that there is an undoubted relationship between the isolation of the Hawaiian chain and the high degree of endemism in its inshore fishes. The third is that the amount of impoverishment of the Indo-West Pacific inshore fauna is roughly correlated with geographic distance from the Indo-Malayan region. Of these three reasons, two will be dealt with later. That concerning Hawaiian endemism is discussed herewith.

That there is a real relationship between the isolation of the Hawaiian chain and the endemism of its fish fauna is not denied. There is, however, no reason to believe that the development of a Hawaiian endemic form re-

quires any great period of isolation. Apparently the time required would be only that necessary for an immigrant species to multiply sufficiently to saturate the available Hawaiian habitat; after this minimum period, any additional immigrants of the same ancestral species would either be eliminated by competition from the previously arrived stock or would interbreed with its members, in which case any genetic difference in the subsequent arrivals would soon be swamped out. (Or, to put this last point conversely, any genetic differentiation that had occurred in the original immigrant stock would be maintained.) In the Hawaiian Islands, instances of what appears to be interbreeding between original and subsequent immigrant stocks are known (Gosline, 1955), but these merely reinforce the basic point made here that water barriers between the Hawaiian chain and other Central Pacific islands are traversable to inshore fishes.

If, within the Central Pacific, fishes are able to get from one island or island group to the next, then the differences in the fish faunas of the various Central Pacific islands must be explained in terms of survival and reproduction around individual islands. (The generally accepted assumption is made here that inshore fishes cannot survive and reproduce in the deep-water areas between islands.) The thesis adopted is that distribution is a function of abundance (Andrewartha and Birch, 1954) and that abundance is a function of habitat (Fig. 2). ("Habitat," as that term is used in this paper, includes all environmental features, physical and

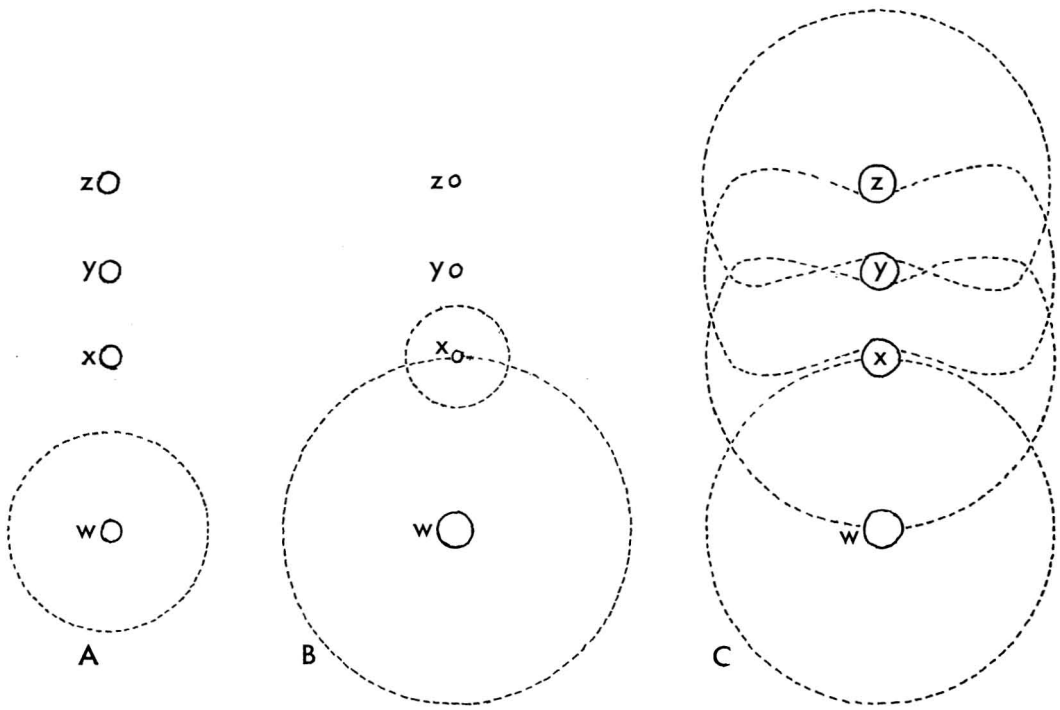

FIG. 2. Diagrammatic representation of the thesis that in the Central Pacific the distribution of inshore fishes is a function of abundance, and abundance a function of habitat (see text). The size of the closed circles represents the extent of favorable environments for a given species on each of four islands (*W*, *X*, *Y*, and *Z*), not the size of the islands. (A large island may have much, little, or no suitable habitat, but a small island may per se limit the amount of favorable habitat.) Dashed lines indicate the extent of dispersal from these islands. In *A* the habitat, hence abundance, at island *W* is inadequate for dispersal to *X*. In *B* the habitat, abundance, and dispersal at *W* are such as to permit the species to reach *X*, but the habitat at *X* limits further spread. In *C* the habitats all permit a general interchange of individuals between islands; the dispersal pattern around *Y* is given a dumbbell shape on the intuitive assumption that individuals dispersing north or south from *Y* would move in to *Z* or *X*, respectively.

biotic, necessary for the successful growth and reproduction of individuals of a species.)

A start with this thesis may be made with the presence of the Hawaiian "endemic" *Apogon menesemus* in the Line Islands. This species is abundant in Hawaii and, parenthetically, has no specialized planktonic larva. The Line Islands records consist of a few specimens taken at Palmyra, the northernmost atoll in the chain. If the collection records can be trusted, the species is not abundant at Palmyra, and is absent from the other Line Islands. The minimum distance from the Hawaiian chain to Palmyra is some 800 miles, but the distance from Palmyra to the next island in the Line group is only 120 miles. Presumably, something about the ecology of the Palmyra inshore areas restricts the populations to such a low point that further migration along the Line Islands is impossible (Fig. 2, column *B*).

Another example of a different geographical but apparently analogous ecological sort is *Salarias fasciatus*. This species is known from the East Indies out in the Central Pacific to the Tuamotus (Chapman, in de Beaufort, 1951, p. 315). It occurs in the southern Marshalls (Strasburg, 1953), but in spite of all the collecting that has been done in the northern Marshalls it appears never to have been taken. In this example again, the distributional limitation seems to have nothing to do with inter-island water barriers, but rather to ecological factors in inshore island areas.

Before continuing it seems well to comment on the relationship between the thesis presented here and the interpretation of collection data. If a species is limited by water barriers, then its presence or absence in a given island would be an all-or-none matter. But if the species is limited by ecological factors within islands, one might expect a gradual restriction of populations near the edges of its range to favorable habitats which might or might not happen to be sampled in any given collection. *Kuhlia* in the Hawaiian Islands provides a good example of this sort of problem. Around Midway it occurs everywhere in great abundance. But at Johnston it is rare and restricted in habitat. It did not appear in any of the inshore poison stations made at Johnston in 1951 (Gosline, 1955). A special and rather strenuous effort had to be made to collect *Kuhlia* at Johnston, and the conclusion would have been drawn from representative inshore collections that it was absent there. Similarly, statements made in this paper on the basis of collections that fish species are "absent" from islands stand subject to revision at any moment.

An aspect of the geography of islands that does seem to be important in the distribution of inshore Central Pacific fishes has to do with what may be called a "filter bridge" effect. If any inshore fish is to move between island groups it seems probable that it would move between the two closest islands in the two groups (Fig. 2, column *C*). But such jumping-off points from one island group to the next are often relatively small outliers of the main chain and, as such, may have neither the size nor the habitat suitable for the development of large populations. Thus Kingman Reef, at the northern tip of the Line Islands, is smaller than the islands farther south. Wake and Johnston are similarly relatively small outliers of the Marshall and Hawaiian islands, respectively. To the extent that the factor discussed above is real, the outermost islands between groups cause a filtering effect on the distribution of species.

Such filtering must also occur among other organisms that make up the biotic environment in which fishes live. In many instances at least it would seem to be the progressive impoverishment of this biotic environment from west to east in the Central Pacific that causes the gradual diminution in the fish fauna. An example of what would appear to be this phenomenon is provided by two rather similar species of *Pomacentrus*. *P. jenkinsi* and *P. nigricans* are both abundant fishes in the northern Marshalls. To the northeast, i.e., in the Hawaiian Islands, *P. jenkinsi* is very abundant, but *P. nigricans* does not occur. To the southeast, in the Line Islands, *P. nigricans* is very abundant, but *P. jenkinsi* has not been taken. One suspects a sorting out (and hence simplification) of habitats in these areas to the east of the Marshalls that no longer permits both of these species of *Pomacentrus* to occur together.

Somewhat the same phenomenon has been previously demonstrated at Johnston (Gosline, 1955). Here, between closely related (counterpart) species, one Hawaiian and one southern, either may occur, but not both.

To add to the difficulty of geographic analysis there are also ecological differences between areas. One type may be considered successional. In the Central Pacific, for example, the Marquesas are apparently relatively new, high islands with slight reef development. The fishes found there seem to be the sort one would expect of such early successional stages in atoll formation. The absence of many reef fishes from the Marquesas and their presence in the nearby Tuamotus is most probably attributable to ecologic rather than geographic conditions.

But even among "mature" atolls there may be differences of habitat between island groups, between the various islands within a group, or between the different areas of a single island. Differences in habitat between the Line and Marshall groups are suggested by the following comparison, which is restricted to "ubiquitous" forms to minimize within-island differences. On Bikini only 27 of the 279 species of inshore fishes were taken at 20 or more stations by Schultz et al. (1953–1966). Of these, 11 were also taken from all three of the Line Islands collected (the best available measure of ubiquity in the Line group). However, six of these 27 Bikini species were not collected in the Line Islands at all: *Parapercis cephalopunctatus, Halichoeres maculatus, Pomacentrus jenkinsi, Acanthurus "elongatus," Siganus rostratus,* and *Naso lituratus,* though one specimen of *Naso lituratus* was seen in the water. The postulate that something about the Line Islands habitat is unpropitious for these six species seems far more probable than that they were unable to get from the Marshall to the Line group. Indeed, a particular ecological factor, the impoverishment of the Line Islands algal flora (de Wreede, personal communication), may explain the absence or rarity of the last four of the six species, for the four are all herbivores.

If the Marshall-Line islands inshore fish fauna is compared with that of Hawaii, other gaps appear. The most notable of these are the absence of *Lutjanus,* the *Gobiodon-Paragobiodon* complex, and inshore species of *Epinephelus* from Hawaiian waters. All of these are carnivores. *Epinephelus* and *Lutjanus* are large, generalized feeders that would seem to have abundant sources of food in Hawaii. *Epinephelus* is actually represented in Hawaii by two native species, but they are relatively deep-water forms. Eteline relatives of *Lutjanus* are abundant in deeper Hawaiian waters, and there seems to be no shortage of gobies other than the *Gobiodon-Paragobiodon* complex in either the inshore or deeper waters of Hawaii. The absence of these three groups of fishes from Hawaiian inshore areas is a most puzzling question, but that their absence is not due to the lack of ability to cross the deep-water area surrounding the Hawaiian chain is strongly suggested by the presence in Hawaii of noninshore *Epinephelus* and of the relatives of *Lutjanus* and *Gobiodon.*

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ERRATA

Volume 24, number 1, January 1970: page 134, the series title should read "Pacific Plant Studies 21"; volume 24, number 2, April 1970: page 245, the series title should read "Hawaiian Plant Studies 31"; volume 24, number 4, October 1970: page 424, in the legend for Figure 3, line 2 should read "Haeckel, 0 cm, R-1, S11/2, X240: *2,* transmitted light; *3,* phase contrast. 4. *Calocyclas virginis* Haeckel,"; page 457, the island name in the title should be "Rotuma."